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Designing Sustainable Landscapes: Modeling Connectivity

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A project of the University of Massachusetts Landscape Ecology Lab

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1 Problem Statement

Our primary mission as conservationists and public stewards of fish and wildlife resources is to ensure the conservation of biological diversity. Thus, our primary over-arching goal is to maintain well-distributed viable populations of all native species and the ecosystem processes they perform and depend on, and the Strategic Habitat Conservation (SHC) approach was developed for the purpose of achieving this goal, but it does not specify how. As described in the ecological integrity document (McGarigal et al 2017), under the auspices of the Designing Sustainable Landscapes (DSL) project, we decided to combine a coarse-filter ecosystem-based approach with the traditional species-based approach.

Connectivity is considered a vital attribute of a landscape (Taylor et al. 1993) and deemed critical to the adaptive capacity (sensu Elmqvist et al. 2003) of a landscape in the face of climate change (Czucz et al. 2011). The disruption of landscape connectivity by human land use activities is considered a principal cause of the decline in biodiversity and is increasingly of concern to conservation scientists (Chetkiewicz et al. 2006, Crooks and Sanjayan 2006, Hilty et al. 2006, Beier et al. 2008). Thus, biodiversity conservation strategies that seek to protect places of high ecological integrity and/or habitat capability without also ensuring viable connections among those places may ultimately be doomed to failure in the face of environmental changes.

In a separate document on ecological integrity, we describe the basis for our ecosystem-based approach in the context of the Landscape Change, Assessment and Design (LCAD) model and describe the details of how we measure ecological integrity. Here, we describe our ecosystem-based assessment of local and regional connectivity, which serves as the basis for identifying conservation focus areas important to the maintenance and/or restoration of local and regional connectivity.

2 Solution Statement

The coarse-filter, ecosystem-based approach to the conservation of biodiversity, as we define it, has two major components: 1) identifying areas of high ecological integrity to serve as "core areas", and 2) identifying areas important for providing connectivity both within and among cores areas.

Connectivity refers to the propensity to facilitate or impede ecological flows (including individuals) across the landscape. Connectivity it is a complex, multi-faceted concept that can be considered from several different perspectives and at different scales, and thus connectivity can be measured in many different ways. Connectivity is incorporated into the resiliency metrics: connectedness and adaptive capacity, as described in the integrity document, whereby greater connectivity confers greater resiliency and thus integrity to cells and greater capacity to adapt to changing environmental conditions.

Connectivity can also be measured directly and more generally without regard to resiliency per se using a suite of metrics that operate at different scales and variously measure the amount of flow through a cell independent of whether the cell has high ecological integrity itself; e.g., a cell of forest surrounded by development but situated between two areas of high ecological integrity where it might act as a "stepping stone" to facilitate movement between the two core areas. In this regard, we measure a suite of connectivity metrics for the purpose of informing landscape design; specifically, to assess and prioritize sites for their importance in conducting flows within and among designated core areas. In addition, we evaluate restoration opportunities associated with restoring or improving connectivity by upgrading culverts (i.e., road-stream crossings), removing dams, and building terrestrial wildlife passage structures across roadways independent of the designated cores created as part of the landscape design.

3 Key Features

Excluding the resiliency metrics (i.e., connectedness and adaptive capacity) described separately in the integrity document, our connectivity assessment includes several measures to address local and regional connectivity, as follows:

- **Local connectivity** — refers to the spatial scale at which individual organisms interact directly with the landscape via demographic processes such as dispersal and home range movements, which we represent at the scale of a few kilometers. Importantly, the local connectivity metrics below are cell-based (i.e., a unique value is assigned to each cell) independent of any core area designation.
    - *Local conductance* — measures the total amount of ecological flow through a cell from neighboring cells as a function of the ecological similarity between the focal cell and the neighboring cells which determines the resistance to flow.
    - *Local vulnerability* — measures the vulnerability of a cell to the loss of high local conductance caused by future development, and is a function of local conductance and the integrated future probability of development.
    - *Critical local linkages* — measures the relative potential to improve local connectedness through restoration, including dam removals, culvert upgrades, and creating terrestrial road passage structures. Each dam, road-stream crossing and road segment is scored based on its potential to improve local connectivity through the corresponding restoration action.
- **Regional connectivity —** refers to the spatial scale at which populations through time interact indirectly with the landscape, which we represent at the scale of 10's of kilometers. Importantly, the regional connectivity metrics below are node-based; i.e., dependent on the designation of core areas. Each cell is assigned a unique value but only with respect to their ability to conduct flows among the designated cores. Thus, our regional connectivity assessment is applicable only in the context of landscape conservation design in which core areas have been designated.
    - *Regional conductance* — measures the total amount of ecological flow through a cell from nearby nodes (i.e., core areas) and is a function of the size and proximity of the nodes and the resistance of the intervening landscape and of the focal cell itself.
    - *Regional irreplaceability* — measures the concentration of ecological flow between nearby nodes going through a cell; it is a function of the proportion of flow paths

between two nodes that go through each cell independent of the size and proximity (up to a limit) of the nodes.

- *Regional vulnerability* — measures the vulnerability of a cell with high regional conductance and concentrated flow to the loss of its connectivity value caused by future development, and is a function of regional conductance, regional irreplaceability and the integrated future probability of development.
- *Critical nodes* — measures the relative contribution of each node (i.e., core area) to regional connectivity; specifically, the change in the connectivity of the entire core area network if the node were removed.
- *Critical linkages* — measures the relative contribution of each linkage (i.e., the set of pathways between each pair of nearby nodes) to regional connectivity; specifically, the change in the connectivity of the entire core area network if the linkage were removed.

There are two important over-arching considerations and/or limitations to our connectivity assessment:

- Our connectivity assessment is ecosystem-based. Specifically, we assess ecological flows from the perspective of the ecological settings or biophysical attributes of the landscape without regards to individual focal species. This is in part due to our desire for a holistic perspective on connectivity, but it also reflects the more pragmatic challenges of trying to model connectivity separately for a large suite of species and then meaningfully integrating the species-specific results into a single biodiversity conservation design. Importantly, we recognize that connectivity is an organism- or process-specific concept, whereby each organism or process interacts with the physical landscape in a unique manner and at a different scale, but the computational demands of modeling connectivity separately for every species given limited time and resources requires that we adopt an ecosystem-based approach, at least for the interim, so long as we recognize the limitations of such an approach. Of course, to the extent that the representative species are representing distinct ecological systems -- one of the major assumptions of the representative species approach -- then the ecosystem-based assessment of connectivity should be an adequate surrogate for the connectivity needs of the individual representative species.
- Given the above, it is important to be aware that our connectivity assessment is not optimized for any single species, either in the way we model ecological flows across the landscape (e.g., the characterization of landscape resistance to movement) or the scale of the process we emulate. Consequently, the places of high local and/or regional conductance, irreplaceability and vulnerability that we identify may not capture the most important or vulnerable connections for any particular focal species. Thus, the results of our connectivity assessment should be viewed with caution when considering the connectivity needs of a single focal species. In future phases, it would be useful to model connectivity separately for each of the representative species and integrate the multi-species connections in a meaningful way.

4 Conceptual Background

The concept of landscape *connectivity* (Merriam 1984) is a key component of our ecological assessment and conservation design and thus figures prominently in the LCAD model. Clarification of several issues pertaining to the concept of connectivity and related terminology is paramount to understanding the LCAD model outputs, and in this regard there are four important issues and distinctions to be made:

4.1 Continuity versus connectivity

The terms *continuity* and *connectivity* are frequently used interchangeably in practice. However, in landscape ecology, there is a subtle yet important distinction between these terms (Crooks and Sanjayan 2006) that we honor in the LCAD model.

- **Landscape continuity** — refers to the physical continuity or structural connectedness of the landscape. For example, landscape continuity as used in practice often refers to the physical continuity of a specific habitat or a particular land cover type across the landscape. In this context, contiguous habitat is physically connected, but once subdivided, it becomes physically disconnected. Habitat continuity is affected both by the amount and spatial configuration of habitat. For example, as habitat patches become smaller and more compact, they extend over less space and thus provide for less physical continuity of habitat across the landscape. To generalize, landscape continuity deals with the physical connectedness of the landscape as perceived or mapped from a particular perspective (e.g., habitat). Note, there are numerous landscape metrics for quantifying continuity.

- **Landscape connectivity —** refers to the functional connectedness of the landscape as perceived by one or more organisms or ecological process. The concept of landscape connectivity has been defined as the “degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993) or as “the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure” (With et al. 1997). Both of these definitions highlight the functional nature of connectivity, by emphasizing the dependence of movement on landscape structure. Furthermore, while these and other definitions emphasize the movement of organisms, the concept of landscape connectivity can be extended to consider more generally the movement of energy, matter, or information (gene flow) across the landscape. Regardless of which currency is used, the greater the degree of movement or flow across the landscape, the greater the overall connectivity of the landscape. Thus, landscape connectivity reflects the interaction of ecological flows (e.g., movement of organisms, energy, materials) with the physical landscape structure (i.e., the composition and spatial configuration of the landscape), and therefore what constitutes functional connectedness clearly depends on the organism or process of interest; for example, patches that are connected for bird dispersal might not be connected for salamander dispersal. Thus, landscape connectivity is affected by landscape continuity, but the magnitude and nature of the affect depends on how the organism or process scales and perceives the landscape. As with landscape continuity, there are a number of landscape metrics or approaches for quantifying connectivity, but all depend on a complex parameterization that depends on knowledge of the focal organism or process.

A central question in landscape management for the conservation of biodiversity and ecological integrity is, "as the physical *continuity* of the landscape is disrupted (through development), at what point does landscape *connectivity* become impaired and adversely impact ecological processes?" In the context of LCAD model, we are largely concerned with *connectivity*, not just continuity per se, but we do so in a generalized manner because we do not have a single focal organism or process. Instead, we are concerned with how myriad organisms and processes collectively respond to the physical continuity of environments. This approach is implemented in our "resistant kernel estimator" methodology discussed in the integrity document that combines the physical distribution of land cover types and ecological settings (i.e., continuity) with the concept of permeability or ecological resistance, whereby each location confers a varying degree of resistance to ecological flows (i.e., connectivity).

4.2 Potential versus actual connectivity

Functional connectivity (or simply connectivity) can be subdivided further into potential versus actual connectivity (Fagan and Calabrese 2006), as follows:

- **Potential connectivity** — uses some basic, indirect knowledge of the potential for movement. In practice, potential connectivity is often assessed using expert opinion on how ecological flows are affected by landscape features, but it can also be assessed more objectively using measured ecological attributes as the basis for determining landscape resistance without explicit regard to any focal species or process.

- **Actual connectivity** — directly quantifies movement rates based on actual observations. In practice, actual connectivity is derived using a variety of data sources and methods to estimate landscape resistance, which then serves the basis for assessing connectivity (Zeller et al. 2012).

The primary difference between potential and actual connectivity lies in the amount of information available on the response of the organism or process to landscape structure. Although assessing the actual connectivity of the landscape might be the goal, we usually do not have sufficient empirical information on how landscape structure influences movement behaviour or other ecological flows across the landscape to permit this level of assessment (Zeller et al. 2012). Thus, most analyses of landscape connectivity are of the potential connectivity of the landscape. In this study, we evaluate potential connectivity, as we do not have empirical data on movement, nor do we have a single species or process on which to focus estimates of movement rates.

4.3 Three faces of connectivity

There are myriad ways to measure the functional (potential) connectivity of a landscape or of a particular landscape unit (e.g., grid cell) within a landscape. In the context of the LCAD model, the functional connectivity of a landscape unit can be assessed from three different perspectives (**Fig. 1**):

- **Traversability** — refers to the connectivity of a focal spatial unit (e.g., grid cell) to its ecological neighborhood (i.e., its landscape context) when it is viewed as a source; in other words, to what extent are ecological flows (e.g., dispersal) outward from that unit impeded or facilitated by the surrounding landscape. For example, to what extent can organisms effectively disperse from that location to other parts of the landscape? If dispersal is highly constrained by impermeable landscape features surrounding that location, the cell is said to have low outflow or traversability. Conversely, if dispersal is relatively unimpeded by the surrounding landscape, the cell is said to have high outflow or traversability. In CAPS, the traversability metric is based on the resistant kernel estimator (described later). Specifically, traversability for a cell is determined by placing a single resistant kernel over the focal cell and comparing the volume of the resulting kernel to that of a standard (i.e., nonresistant and homogeneous neighborhood) kernel placed over the same cell. The ratio is an index of traversability.

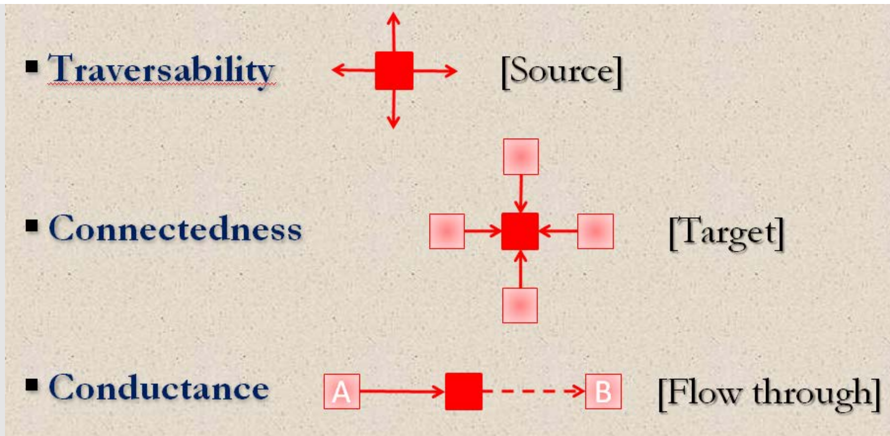

Figure 1. Schematic diagram of the three "faces of connectivity": traversability, connectedness, and conductance.

- **Connectedness** — refers to the connectivity of a focal spatial unit (e.g., grid cell) to its ecological neighborhood (i.e., its landscape context) when it is viewed as a target; in other words, to what extent are ecological flows (e.g., dispersal) to that unit from ecologically similar neighbors impeded or facilitated by the surrounding landscape. For example, to what extent can organisms from similar ecological settings in the surrounding landscape disperse to that location? If the cell is unable to receive many dispersers, it is said to be highly isolated and have low connectedness, and vice versa. Connectedness is related to traversability, but the latter refers to the outflow from the focal cell (i.e., when viewed as a source) whereas the former refers to the inflows to the focal cell (i.e., when viewed as a target) but with the added constraint that it considers the ecological similarity of the neighboring cells from which the flows are originating. In LCAD, we measure connectedness in association with our assessment of local resiliency. Specifically, connectedness for a cell is determined by placing a single resistant kernel over each neighboring cell and multiplying it by the ecological similarity to the focal cell, summing all the overlapping kernels at the focal cell, and comparing the resulting value to that expected in a nonresistant and homogeneous ecologically similar neighborhood. The ratio is an index of connectedness and a measure of resiliency. Note, we also measure adaptive capacity in a similar fashion (i.e., inflows to the focal cell), but with the added constraint that it considers the ecological similarity of the neighboring cells in the future from which the flows are originating.

- **Conductance** — refers to the degree to which a focal spatial unit (e.g., grid cell) impedes or facilitates ecological flows between other spatial units; in other words, to what extent does a focal cell play a role in connectivity between point A and point B, or to what degree does a focal cell function as a thruway for flows between point A and point B. The conductance of any cell is a function of its permeability (or resistance) to ecological flows as well as its strategic position in the landscape between A and B. For example, a wildlife passage structure on an expressway may be quite permeable to wildlife crossings, but if it is not located along an important movement route between A and B, it will not function to promote the linkage of A and B. Thus, conductance deals with the role of each location in conferring connectivity to the broader landscape.

In the context of the LCAD model, we are concerned with all three faces of connectivity. For the purpose of assessing the ecological integrity and adaptive capacity of a grid cell, we are principally concerned with the issue of connectedness and traversability, since these largely affect the resiliency of the cell to disturbance and stress and its ability to adapt to changing environmental conditions over time. The issue of conductance is relevant in determining the value of a cell in maintaining or enhancing the integrity of the surrounding landscape rather than determining the integrity or adaptive capacity of the cell itself; i.e., its role in facilitating flows between other places. Importantly, a cell may have low integrity and high conductance and thus be important to the conservation of biodiversity at the landscape scale even though it otherwise lacks integrity itself. Consequently, conductance does not enter into the computation of the local index of ecological integrity or adaptive capacity. Rather, it is used in the context of assessing local connectivity among neighboring cells and regional connectivity among a set of core areas (nodes).

4.4 Local versus regional connectivity

Third, "what ultimately influences the connectivity of the landscape from the organism's perspective is the scale and pattern of movement (scale at which the organism perceives the landscape) relative to the scale and pattern of patchiness (structure of the landscape)" (With 1999). As this passage indicates, connectivity is a scale-dependent concept and there is no one right scale for assessing connectivity, because ultimately it depends on the organism or process under consideration. In the context of the LCAD model, although we are dealing with connectivity from an ecosystem-based perspective without explicit reference to any single species, it is still useful to consider species' needs with respect to selecting the scale or scales of assessment. Unfortunately, it is impractical to examine connectivity at every relevant scale to meet the needs of the full suite of species associated with the various ecosystems. As a practical compromise, we identify two scales for assessing connectivity, which we refer to as *local* and *regional* scales, as follows:

- **Local connectivity —** refers to the spatial scale at which individual organisms interact directly with the landscape via demographic processes such as dispersal and home range movements. This is the landscape context that an individual organism might experience during their lifetime. In choosing the spatial scale(s) for the local connectivity assessment (using the resistant kernel estimator), we incorporate two important considerations. First, we generally focus on vertebrates, largely because their life history and habitat use patterns are better understood than many plants and invertebrates and because they are more often the focus of conservation concerns. Second, we generally focus on the average maximum movement distances of a suite of organisms; in other words, we do not use the maximum movement distance of a single "indicator" species nor do we bias the result towards the most vagile organisms. In the context of the LCAD model, the spatial scale for the local connectivity assessment is in the range of a few kilometers, but it remains a flexible parameter.

- **Regional connectivity** — refers to the spatial scale at which populations through time interact indirectly with the landscape. This is the scale at which long-term ecological processes such as range expansion/contraction and gene flow occur. At this scale, individuals generally do not interact with the landscape over the course of their life, but their offspring or their genes might over multiple generations. Consequently, there is no real upper limit on the regional scale; the longer the time frame, the larger the regional scale at which the landscape structure matters. In the context of the LCAD model, the spatial scale for the regional connectivity assessment is in the range of 10's of kilometers, but it too remains a flexible parameter up to some limit imposed by computational resources. Importantly, the scale of the regional connectivity assessment is several times larger than the scale of the local connectivity assessment.

In the context of the LCAD model, we are concerned with both local and regional connectivity. Local connectivity is relevant to the ecological integrity of each grid cell and is adopted in the measurement of connectedness (and incorporated into the local *Index of Ecological Integrity, IEI*) and adaptive capacity. In addition, local conductance reflects the magnitude of flow through a cell based on its landscape context and is used here as an independent measure of a cell's contribution to local connectivity independent of its ecological integrity or adaptive capacity. All three metrics are computed for each cell independent of any designated core area network. Regional connectivity is relevant to the ecological integrity of the landscape as a whole and is used in the context of assessing regional connectivity among a set of conservation core areas (nodes) that is central to our landscape conservation design approach (McGarigal et al 2017).

5 Detailed Description of Process

Our connectivity assessment is done at two scales: local and regional, and produces a suite of metrics representing various perspectives on connectivity. In the calculation of these metrics there are several important considerations:

- Most of the metrics are computed at the cell level; i.e., they measure conductance, irreplaceability or vulnerability of the local site (cell) and logically produce a grid. However, some of the metrics are non-spatial in the sense that they produce a numerical score for each conservation unit (e.g., core area or linkage between cores) or for the landscape as a whole.

- All of the metrics described here are computed for a static snapshot of the landscape; i.e., they measure the connectivity of the landscape based on the conditions in the landscape at a single point in time, even though they are intended to identify places important for maintaining connectivity over time.
- The metrics described here measure connectivity at either the local scale or regional scale. The local connectivity metrics measure connectivity for every cell based on attributes of the cell and its local neighborhoood (i.e., its landscape context) at the scale of one to a few kilometers independent of any designated core area network. The regional connectivity metrics measure connectivity based on a designated core area network at the scale of 10's of kilometers. The regional connectivity metrics variously measure the conductance, irreplaceability and vulnerability of cells, but only in relation to their context in the designated core area network, and some of the metrics apply to the core area or link between core areas as the spatial unit rather than individual cells. Consequently, the regional connectivity metrics are relevant only in the context of landscape conservation design in which core areas have been designated to achieve specified conservation targets.
- The metrics described here measure connectivity from an ecosystem-based perspective without explicit reference to individual species. Landscape resistance, which forms the basis for modeling ecological flow across the landscape, is based on the differences in ecological settings between cells and not on how any particular species perceives the environment. The ecological settings variables are a multivariate set of biophysical attributes that describe the abiotic, biotic and anthropogenic environment of each cell. The consequence of this is that the connectivity assessment is not optimized for any particular species; indeed, the connectivity of the landscape for any particular species could be very different from the connectivity we measure, depending on how and the scale at which the species' perceives and responds to environmental conditions during movement. Note, our modeling approach is amenable to individual species-based modeling, but for practical reasons we have not implemented separate connectivity models for each representative species. This should be an important focus for a future phase of this project.

5.1 Local conductance

Local conductance measures the total amount of ecological flow through a cell from neighboring cells as a function of the ecological similarity between the focal cell and the neighboring cells. Local conductance differs slightly from local connectedness in that conductance measures how much flow there is to and through a cell from neighboring cells independent of the ecological similarity of the focal cell to its neighbors, whereas connectedness measures how much flow there is to the focal cell from ecologically similar neighboring cells. Thus, the conductance of a focal cell is determined in a sense by the average resistance of its neighborhood across all the ecological settings, whereas the connectedness of a focal cell is determined largely by the ecological similarity of its neighborhood. However, in practice these two measures tend to be highly correlated. Conceptually, these two metrics have different interpretations and uses. Connectedness is a measure of ecological isolation. Connectedness confers resiliency to a site in the short-term, since being connected to similar ecological settings should promote recovery of the constituent organisms following a local disturbance. Conductance, on the other hand, is a measure of importance in promoting ecological flows across the local landscape, regardless of whether the cell itself is highly connected to an ecologically similar neighborhood. Thus, a cell can have high conductance and low connectedness, at least theoretically, although this tends not to happen too often in real landscapes.

Local conductance is computed as the overlap at the focal cell of *resistant* Gaussian kernels derived for every neighboring undeveloped cell (see technical document on Integrity for a detailed description, McGarigal et al 2017), briefly as follows:

1. For each undeveloped focal cell, build a resistant Gaussian kernel (2 km bandwidth, extending out to a maximum distance of 4 km) for all neighboring cells;
2. divide by the maximum value in step 2 for a nonresistant (i.e., resistance = 1 everywhere) and homogeneous ecologically similar neighborhood,
3. cumulatively sum the resulting kernel at each neighboring cell; and let this be the local conductance index.

In step 1 above, the resistance between the focal cell and each neighboring cell is based on weighted Euclidean distance in multivariate ecological setting space as described in detail in the integrity document.

As defined above, local conductance is influenced strongly by how much undeveloped land there is within the local neighborhood of a focal cell, since a resistant kernel is built for each neighboring undeveloped cell but not for developed cells. The ecological similarity of the neighborhood also influences the value of the metric. All other things being equal, an ecologically similar neighborhood will produce larger kernels and increase the conductance through the focal cell, but the degree of ecological similarity of the neighborhood probably has much less impact on local conductance than the amount of development. In addition, since the amount of development and the ecological similarity of the neighborhood influence both local conductance and local connectedness, these two metrics differ only subtly and in most cases a cell with high connectedness will also have high conductance. However, there are situations in which a cell can have high conductance but low connectedness. Specifically, if a focal cell is surrounded by undeveloped but ecologically very dissimilar settings, the conductance could be relatively high because there is still a lot of unimpeded flow getting to the focal cell, but the connectedness of the focal cell itself could be very low because of its low ecological similarity to the neighboring cells. However, a focal cell surrounded by homogeneous identical ecological conditions would have both a connectedness and conductance score of 1 and, for example, a focal cell surrounded by a sea of development would have both a connectedness and conductance score of 0.

The local conductance metric has two primary uses. First, local conductance is a cell-based measure of local connectivity that is independent of any designated core area network (**Fig.2**). Thus, this product can be used to identify places that confer connectivity at the local scale (few kilometers) independent of designated core areas and any formal landscape conservation design. Second, local conductance can be used in combination with designated core areas in the context of landscape conservation design to identify priority areas for conservation action within designated cores.

5.2 Local vulnerability

Local vulnerability measures the vulnerability of a cell to the loss of high local conductance caused by future development as a function of the cell's current local conductance and integrated future probability of development. Local vulnerability identifies places that currently have high local conductance but that are at high risk of development in the future. Cells with relatively low local conductance have low vulnerability regardless of risk of development, since local connectivity will not be degraded too much if they get developed. On the other hand, cells with relatively high local conductance will have high vulnerability if they suffer high risk of development, since local connectivity will be seriously degraded if they get developed.

Local vulnerability is computed as the product of local conductance and the integrated probability of development. The latter can only be fully understood by understanding our urban growth model (see technical document on Urban Growth for a detailed description, McGarigal et al 2017), but briefly it is computed as follows:

1. We divide the landscape up into non-overlap square panes (5km x 5km) and then for each pane we define an (overlapping) window of nine panes centered on the focal pane. This overlapping window approach ensures that we avoid ending up with arbitrary edges or abrupt changes in probability of development along the edges of the panes.
2. Currently, we limit the model to only one of the six possible transition types: 1) undeveloped to low density development, which represents the vast major of the development transitions, although the model could be extended to include the other possible development transitions that are much less likely: 2) undeveloped to medium density development, 3) undeveloped to high density development, 4) low density development to medium density development, 4) low density development to high density development, and 6) medium density development to high density development.
3. Based on the configuration of the window it matches the application window to 3 training windows and creates a weighted average probability of development based on the 3 logistic regression models built in the training windows. This surface is relative and only comparable among cells within the same pane. Essentially, for each 5km square pane, we build 3 logistic regression models based on the models fit from the 3 most similar windows with training data (as described in the urban growth document), and model average the predictions.

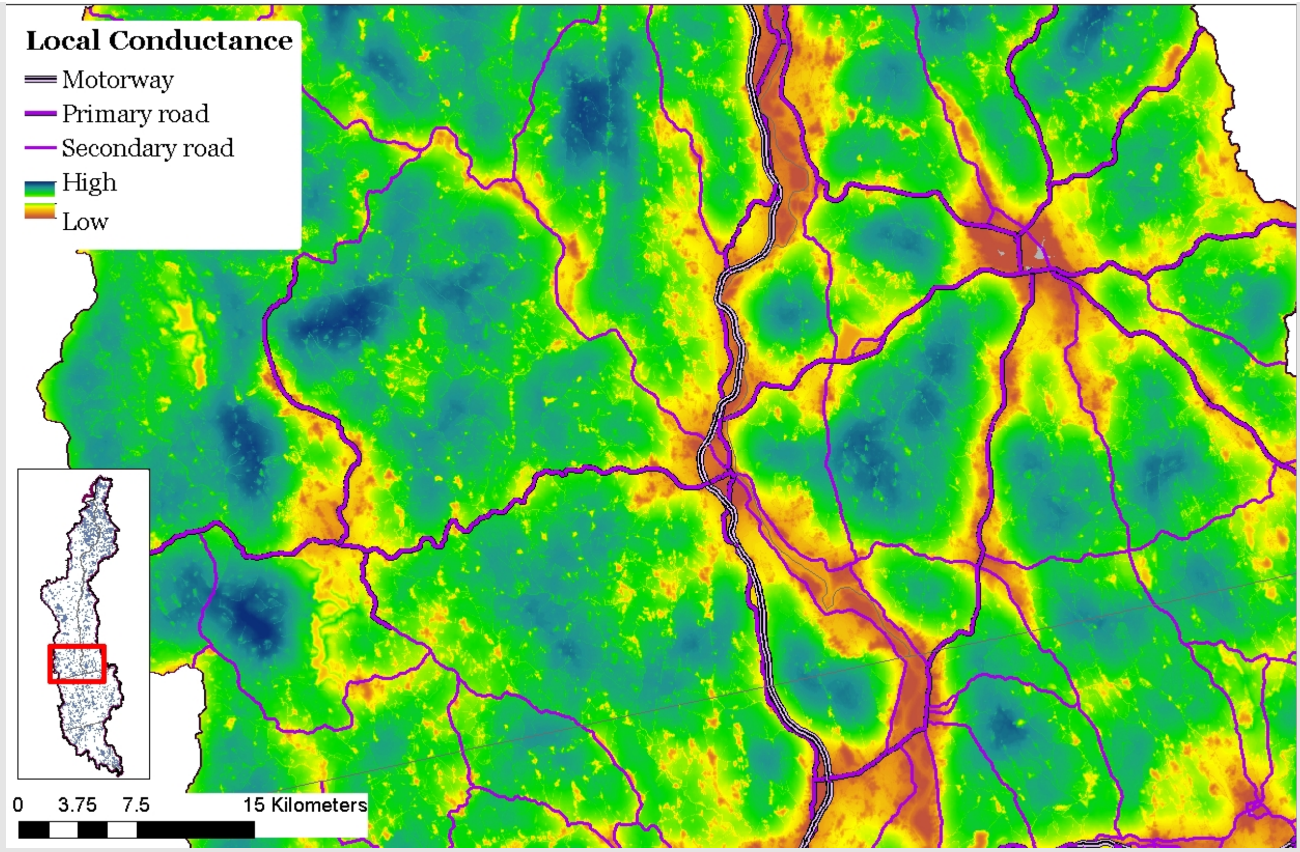

Figure 2. Illustration of the local conductance metric. The areas shown in blue depict relatively high local conductance, whereas the areas shown in red depict relatively low local conductance; major roads are depicted by class.

4. We allocate the number of cells of development (for the undeveloped to low density development transition only currently) based on the projected amount of development in the sub-region the window falls within and the amount that the matched training windows received historically. The sub-regions are defined by aggregating counties into the US Census Bureau CBSAs (Core Base Statistical Areas) or using the county if it falls outside of a CBSA.

5. Given the framework above, to calculate a development probability surface that is smooth (i.e., doesn't not show pane edges as an artifact of our tiling scheme), comparable across the landscape, and indicative of the cumulative probability of development over time between 2010 and 2080, we do the following:

6. for a transition type and window, create the relative probability of development initiation as implemented in the urban growth model;

7. mask out undevelopable cells, including roads, wetlands, conserved land, already developed, etc. to enforce a zero probability of development for these cells;

8. divide the window by the sum of the probability of development in the central pane (5km x 5km). Note, this normalizes the probabilities so that they sum to 1 for each

pane in order to focus on the relative distribution of future development within the pane based on local landscape features. In other words, we now have the relative probability of development for this transition within the pane at the cell level;

9. calculate the probability of each cell being developed (Pt) for this transition given the number of cells of development for this transition allocated to the pane as:

$$P_t = 1 - (1 - P_t^*)^n$$

where Pt* = the normalized probability from step 3 for the tth transition type, and n is the number of cells allocated to the central pane for this transition. Note, for the central pane we now have the actual probability of development for this transition occurring sometime between 2010-2080 at the cell level. Note, here the probability applies to the cell as if we were to develop cells individually, rather than in patches (as actually happens in the real world and in our urban growth model), which is an approximation that we find acceptable for this particular application. For the outer panes we have an extension of that same surface;

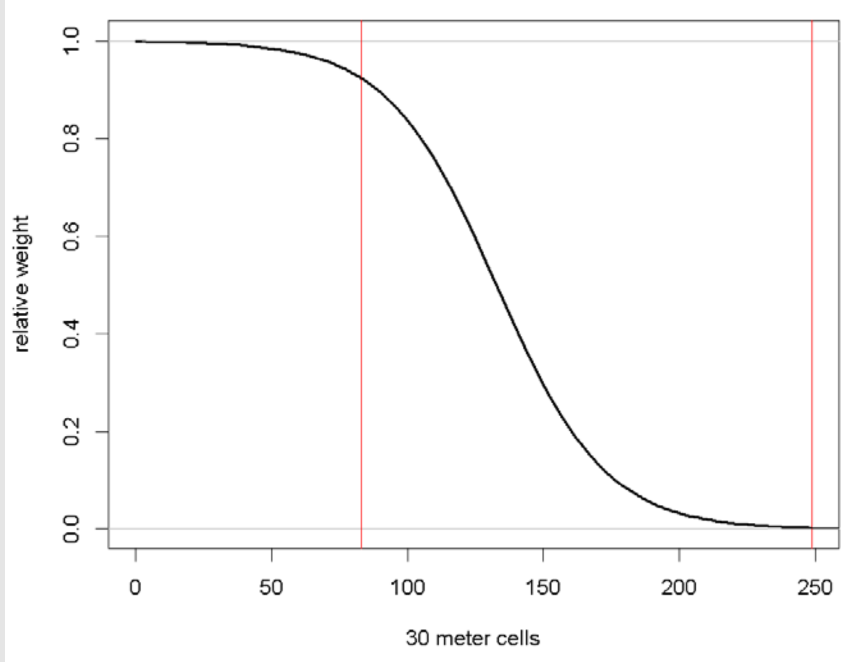

Figure 3. The logistic function used to determine the relative weight assigned to cells in the window based on their distance (in cells) from the center of the window. The red lines represent the distance to the edge of the central pane and the edge of the window orthogonally from the center.

10. calculate weights for each cell in the window based on a logistic function of the distance to the center of the window (**Fig. 3**) as:

$$W_t = \frac{1}{1 + e^{-(b \cdot (x-c))}}$$

where: b=0.05, c=0.8*s, s=the panesize=166 cells, and x=distance (m) to the center of the window;

11. add the weights for the window to a grid of total weights used;

12. add the product of the weights and the probability surface for the window (from step 4) to an intermediate grid;

13. repeat 1 through 7 for every window;
14. divide the intermediate grid by the weights grid to get a continuous probability of development surface for this transition. Note, in this grid each cell is a weighted sum of the probability of development in the 9 windows that overlap it; the weights being a logistic function of the distance to the center of each window;
15. repeat steps 1:9 for each of the six transition types; and
16. calculate a weighted joint probability of development (across all transition types) as:

$$1 - \sum_{t=1}^{6} \left(1 - (P_t \cdot W_t)\right)$$

As defined above, local vulnerability is greatest where there is high local conductance; i.e., in ecologically similar areas with minimal current development, but that have relatively high probability of development. Thus, places with high vulnerability tend to occur in the least developed areas within the urban sprawl zone -- outside the urban centers that already have low local conductance but close enough to the urban centers to have high probability of development in the future.

In the context of the LCAD model, we use local vulnerability for two purposes. First, similar to local conductance, we use local vulnerability as a cell-based measure of risk to local connectivity that is independent of any designated core area network (**Fig.4**). This product can be used to identify places that warrant high priority for conservation action (e.g., land protection) to ensure local connectivity. Second, similar to local conductance, we use local vulnerability as a cell-based measure of vulnerability within designated core areas in combination with regional vulnerability between the core areas (as described below) in the context of landscape conservation design.

5.3 Critical local linkages

Our critical local linkages assessment measures the relative potential to improve local connectivity through restoration, including dam removals, culvert upgrades, and creating terrestrial road passage structures. Each dam, road-stream crossing and road segment is scored based on its potential to improve local connectivity through the corresponding restoration action, but only where it matters -- in places where the current ecological integrity is not already seriously degraded too much.

Our critical local linkages assessment is based on the connectedness metric and its aquatic counterpart, aquatic connectedness, as described in detail in the integrity document. Briefly, connectedness (and aquatic connectedness) represents the amount of ecological flow to the focal cell from neighboring cells, weighted by their ecological distance (as represented by the kernel shape and width) and their ecological similarity (as represented by the similarity weights). Note, underlying this metric is the assumption that ecological flows from similar ecological communities is more important to local connectivity (at least in the short term) than those from dissimilar communities. Importantly, in the calculation of resistance to ecological flows, anthropogenic landscape features are weighted heavily. In

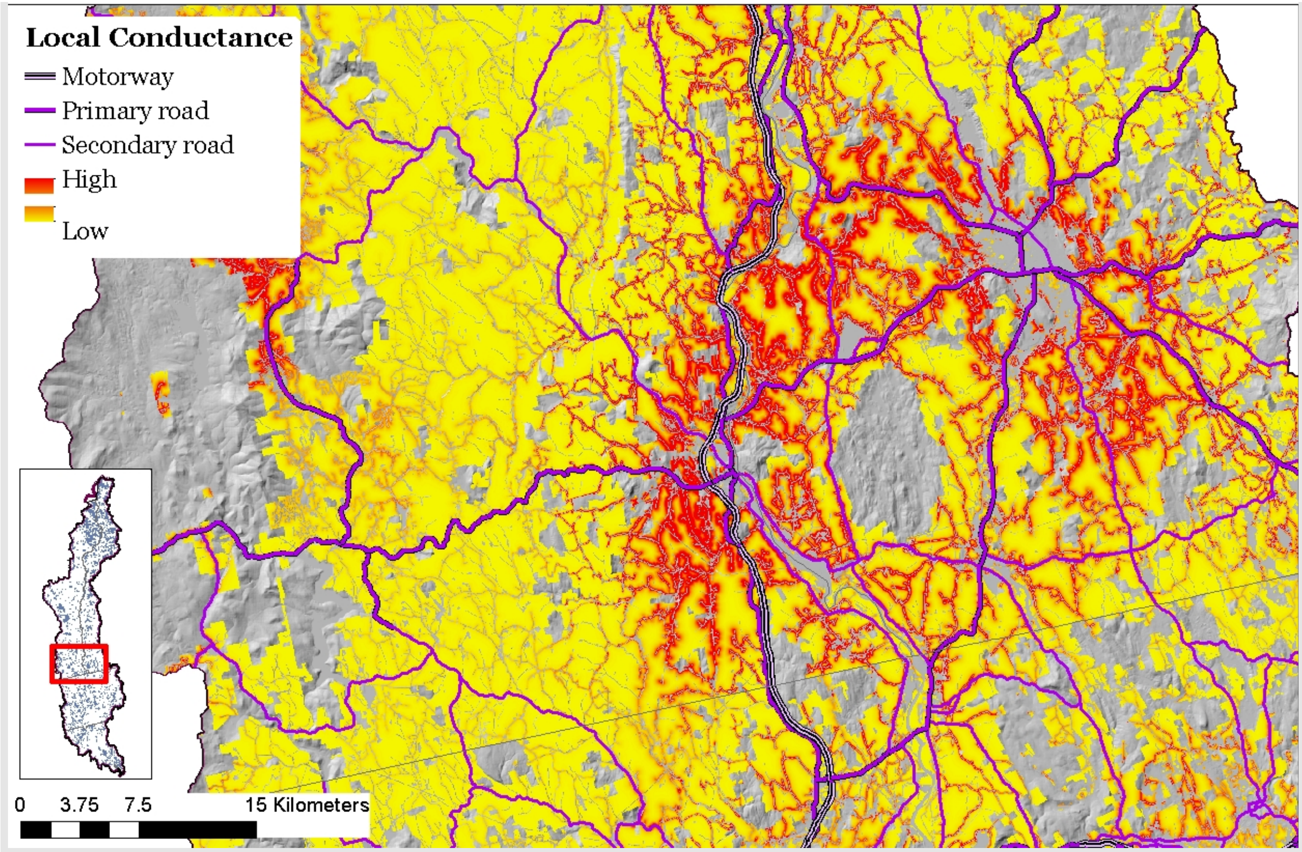

Figure 4. Illustration of the local vulnerability metric. The areas shown in red depict relatively high local vulnerability to future development, whereas the areas shown in yellow depict relatively low local vulnerability to future development; areas already developed or secured from development are transparent; major roads are depicted by class.

particular, road traffic, terrestrial barriers, impervious surface and development all weigh heavily in determining terrestrial connectedness, and aquatic barriers (i.e., dams and road-stream crossings) weighs heavily in determining aquatic connectedness.

Our current critical local linkage assessment involves evaluating the restoration potential of: 1) dam removals, 2) culvert/bridge upgrades and 3) construction of terrestrial wildlife passage structures on roads, as follows:

5.3.1 Dam removals

For the dam removal scenario, we systematically remove each dam, one at a time, and compare the change in aquatic connectedness resulting from the dam removal. Note, each dam has an aquatic barrier score based either on dam height or attributes indicating whether the dam has a partial/complete breach. Specifically, we compute the dam restoration scores as follows:

1. for each dam, compute the baseline aquatic connectedness metric with the dam in place for every cell within the affected neighborhood of the dam (i.e., any cell whose aquatic connectedness value is influenced by the dam);
2. remove the dam (virtually) by setting the aquatic barrier score to 0 and recompute the aquatic connectedness metric for each cell within the affected neighborhood;
3. compute the delta, or difference, in aquatic connectedness score before and after the dam removal for each cell within the affected neighborhood;
4. multiply the delta value by the baseline *IEI* value for each cell within the affected neighborhood; and
5. sum the values above across all effected cells and let this be the restoration score for the dam.

Note, step 4 above involves multiplying the delta aquatic connectivity score by the current *IEI* score for each cell within the affected neighborhood of the dam. This means that an absolute delta of say 0.4 in an area with an average *IEI* of say 0.1 would end up with a much lower dam restoration score than the same delta in an area with an average *IEI* of say 0.9. This makes sense in most cases because it is unlikely to implement a costly dam removal in places that are already so degraded that it won't matter that much. Conversely, if the dam removal occurs in an area that is otherwise in good condition but depressed by the dam, then the potential ecological benefits might be much greater.

The restoration score is an index of the potential improvement in local aquatic connectedness to be achieved in places where it matters most (where the current ecological integrity is not already severely degraded) if the dam were removed. Based on these restoration scores, dams can be ranked and prioritized for restoration (**Fig 5**). Note, these dam restoration scores do not take into account other socio-economic considerations, such as whether the impoundment is a public drinking water supply, that ultimately will determine the cost-benefit tradeoffs of any particular dam removal.

It is important to be aware of two major sources of uncertainty in the dam restoration scores:

- Data gaps and errors inherent in the source data are a major concern. Unmapped dams certainly exist and effect the real-world aquatic connectivity not reflected in our scores. Incomplete and/or inaccurate data on dam height, presence of a fish ladder, and other attributes (such as the partial breach of the dam) result in incorrect estimates of aquatic passability, and for many dams with incomplete data, especially the smaller dams, we are forced to make an assumption about dam height and also to assume that the dam has not been breached and does not have a fish ladder of any kind. Thus, the actual restoration potential of a dam may be quite different than the modeled estimate.

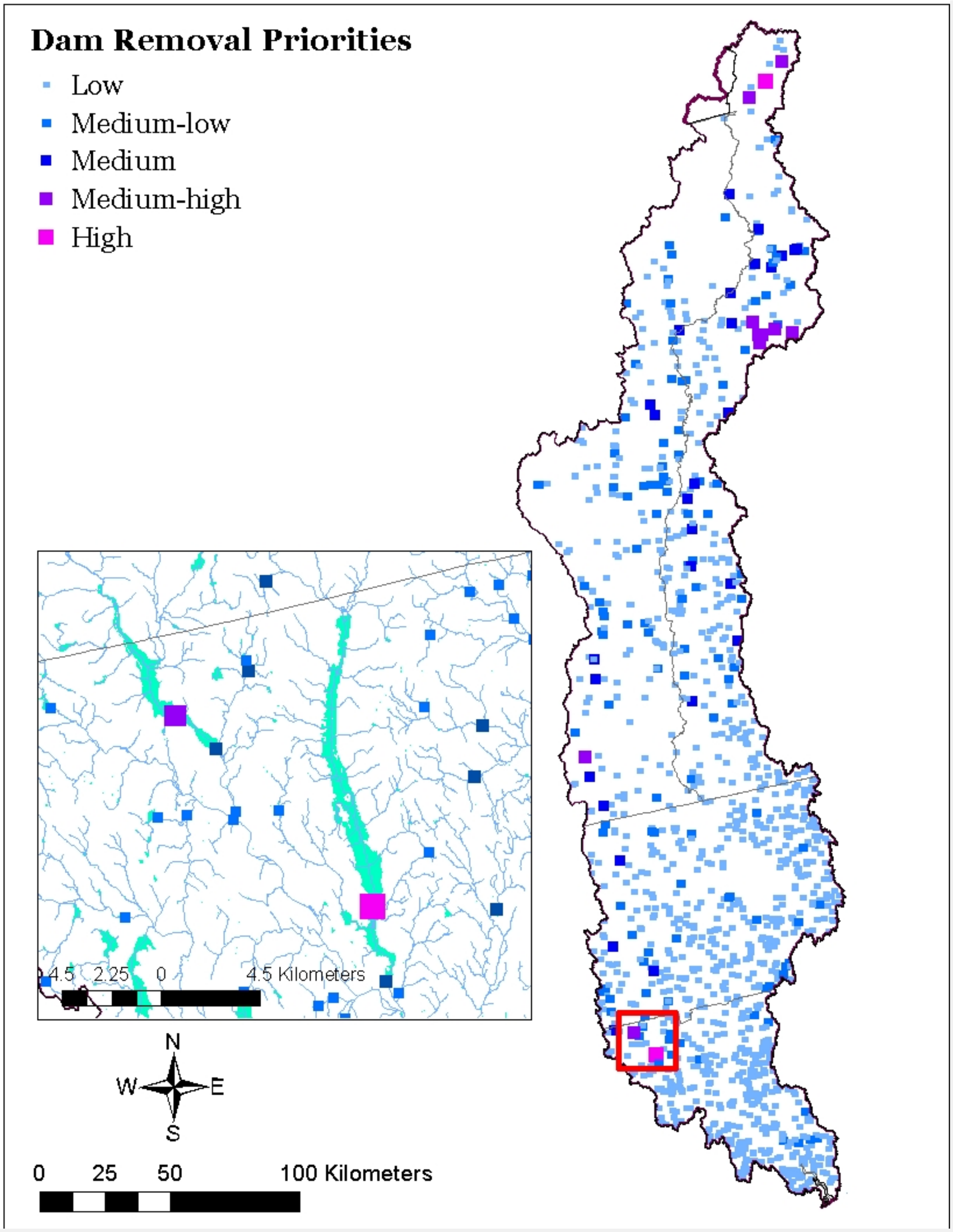

Figure 5. Illustration of the critical local linkage scores for dam removals in the Connecticut River watershed. The size of the symbol represents the relative magnitude of increase in local aquatic connectivity from removing the dam.

- The dam restoration score represents the potential gain in local aquatic connectivity from removing each dam without considering other potential nearby restoration actions to improve connectivity. Of course, dams often don't exist as isolated barriers. The restoration score of a dam is dependent to some extent on the degree to which road-stream crossings nearby on the same waterway are acting as barriers to movement. For example, removal of a dam will result in less improvement in connectivity if there is an undersized culvert a short distance from the dam compared to that same dam but with no other movement barriers nearby (e.g., a bridge instead of a culvert). The undersized culvert will continue to depress aquatic connectedness values even after the dam is removed. Unfortunately, evaluating the combined (and possibly synergistic) effect of multiple restoration activities, such as removing the dam and upgrading the nearby undersized culverts, is computationally extremely challenging and thus we did not attempt here. This remains an important item for future model improvement.

5.3.2 Culvert upgrades

For the culvert upgrades scenario, we systematically upgrade each culvert, one at a time, to a bridge having the minimal aquatic barrier score and compare the change in aquatic connectedness resulting from the culvert replacement. Note, each road-stream crossing has an aquatic barrier score based either on an algorithm applied to field measurements of the crossing structure or predictions from a statistical model based on GIS data. Specifically, we compute the road-stream crossing restoration scores as follows:

1. for each road-stream crossing, compute the baseline aquatic connectedness metric with the existing crossing structure in place for every cell within the affected
2. neighborhood of the crossing (i.e., any cell whose aquatic connectedness value is influenced by the crossing);
3. replace the crossing structure (virtually) with a bridge having the minimum aquatic barrier score (0) and recompute the aquatic connectedness metric for each cell within the affected neighborhood;
4. compute the delta, or difference, in aquatic connectedness score before and after the culvert upgrade for each cell within the affected neighborhood;
5. multiply the delta value by the baseline *IEI* value for each cell within the affected neighborhood; and
6. sum the values across all effected cells and let this be the restoration score for the road-stream crossing.

The restoration score is an index of the potential improvement in local aquatic connectedness to be achieved in places where it matters most (where the current ecological integrity is not already severely degraded) if the crossing structure were replaced with a properly sized bridge. Based on these restoration scores, road-stream crossing structures can be ranked and prioritized for restoration (**Fig. 6**).

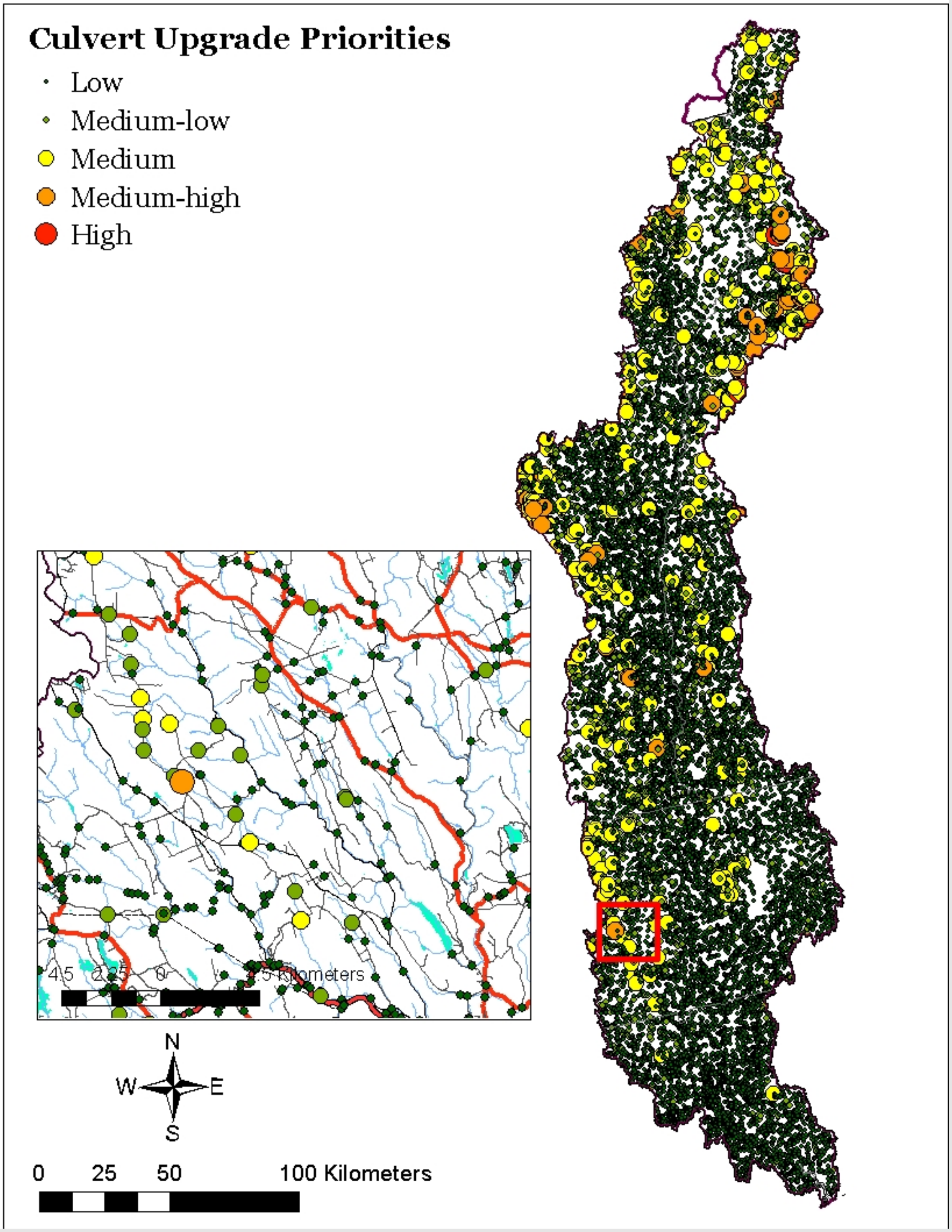

Figure 6. Illustration of the critical local linkage scores for road-stream crossings in the Connecticut River watershed. The size of the symbol represents the relative magnitude of increase in local aquatic connectivity from replacing the culvert with a bridge.

As with dams, it is important to be aware of the major sources of uncertainty in the road-stream crossing restoration scores:

As with dams, data gaps and errors inherent in the source data are a major concern. There exist phantom road-stream crossings erroneously generated by the intersection of roads and streams data in GIS. Perhaps the biggest concern is the lack of information about aquatic passability for most road-stream crossings. Less than 2% of the road-stream crossings within the Northeast region (11,118/584,245) have been assessed in the field. We use this field-based assessment where it exists, but for the vast majority of road-stream crossings that have not been assessed in the field we are obligated to predict aquatic passability based on a statistical model using GIS data as the predictors. Not surprisingly, the performance of this model is not great. We incorrectly predicted a bridge to be a culvert ~45% of the time (omission error) and we incorrectly predicted a culvert to be a bridge ~6% of the time (commission error), with the latter errors being more problematic because we end up predicting a much greater passability score than possible for a culvert. Overall, the predictions of aquatic passability scores are extremely noisy (adjusted R^2=0.26). Thus, the actual restoration potential of a road-stream crossing may be quite different than the modeled estimate. Fortunately, there is a region-wide effort underway to expand the field-based assessments (North Atlantic Aquatic Connectivity Collaborative (NAACC)) and these results will be incorporated as they become available in a future phase of this project.

The road-stream restoration score represents the potential gain in local aquatic connectivity from upgrading each road-stream crossing to a bridge with the minimum aquatic barrier score without considering other potential nearby restoration actions to improve connectivity. Of course, road-stream crossing often don't exist as isolated barriers. The restoration score of a road-stream crossing is dependent to some extent on the degree to which road-stream crossings and dams nearby on the same waterway are acting as barriers to movement. For example, upgrade of a culvert will result in less improvement in connectivity if there is a dam or an undersized culvert a short distance from the crossing compared to that same crossing but with no other movement barriers nearby. The dam or undersized culvert will continue to depress aquatic connectedness values even after the target culvert is upgraded. Unfortunately, evaluating the combined (and possibly synergistic) effect of multi-structure restoration scenarios, such as upgrading all nearby undersized culverts, is fraught with several computational challenges and thus we did not attempt it here. This remains an important item for future model improvement.

For the road-stream crossings assessed in the field, we used an assessment protocol and scoring system developed by the North Atlantic Aquatic Connectivity Collaborative (NAACC) and its predecessor, the Stream Continuity Project, for scoring crossing structures according to the degree of obstruction they pose to aquatic organisms. Of course, as with any such algorithm, it cannot deal effectively with the myriad species-specific constraints on passability that affect the entire aquatic community. Thus, the score must be viewed as a generalized index on aquatic passability and cannot be used to infer passability for any single species.

5.3.3 Terrestrial wildlife road passage structures

For the terrestrial wildlife road passage structure scenario, we systematically locate a road crossing structure on road segments, one at a time, and compare the change in (terrestrial) connectedness resulting from the passage structure. Note, each road-stream crossing has a terrestrial barrier score (in addition to an aquatic barrier score) based either on an algorithm applied to field measurements of the road-stream crossing structure or predictions from a statistical model based on GIS data. Specifically, we compute the road passage restoration scores as follows:

- for each 300 m segment of road (see below), compute the baseline connectedness without the road passage structure for every cell within the affected neighborhood of the road segment (i.e., any cell whose connectedness value is influenced by the road segment);
- install the road passage structure (virtually) by reducing the value of the terrestrial barrier and Gibbs traffic settings variables by 90% for the road cells associated with the road segment and recompute the connectedness metric for each cell within the affected neighborhood;
- compute the delta, or difference, in connectedness score before and after the road passage structure is installed for each cell within the affected neighborhood;
- multiply the delta value by the baseline *IEI* value for each cell within the affected neighborhood; and
- sum the adjusted deltas across all effected cells and let this be the restoration score for the road segment.
- Because of the large number of road cells in the Northeast and the computational intensity of the Critical Linkages analysis, we only run the roads analysis for a subset of road cells. Specifically, we exclude roads with Gibbs-transformed traffic rates <0.25 on the assumption that wildlife passage structures would be unlikely to be targeted to smaller roads. We also exclude all road cells in urban areas, identified by having >20% cells classified as roads within a 1 km circle, on the assumption that wildlife passage structures would be unlikely to be targeted to highly urbanized areas since the potential benefit of a passage structure would be minimal. Lastly, we assess 300 m road segments not only for computational efficiency, since this involves assessing one-tenth as many units as doing every cell, but also because modern road passage structure are often quite large and include some form of drift fencing that may extend 300 m or more to funnel wildlife to the crossing. Note, the 300 m road segments also account for divided highways where they exist so that both sides are always included in the same segment, such that a passage structure on a divided highway would actually involve building a passage under both sides of the divided highway.

The restoration score is an index of the potential improvement in local terrestrial connectedness to be achieved in places where it matters most (where the current ecological integrity is not already severely degraded) if the road crossing structure were installed.

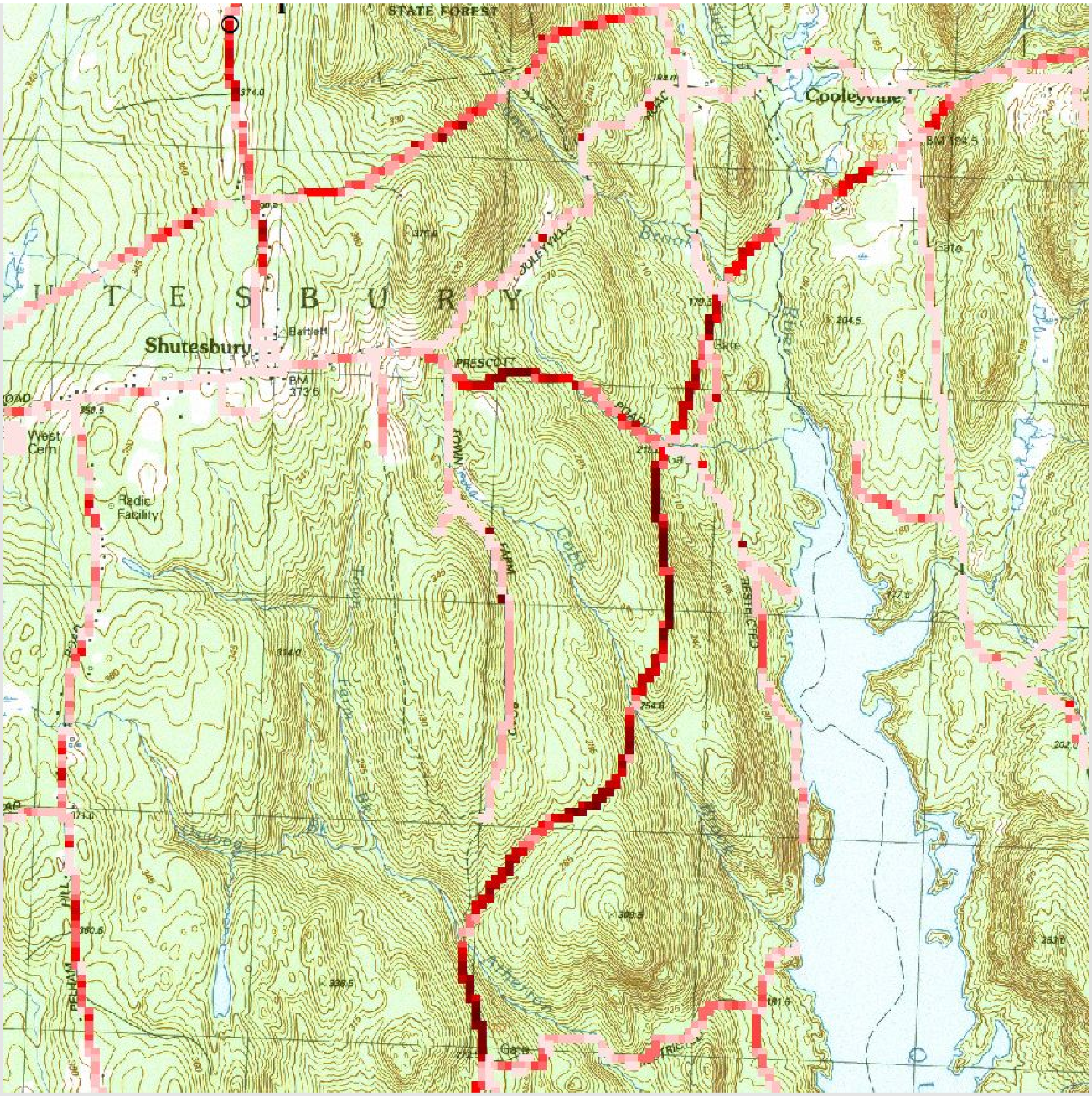

Figure 7. Illustration of the critical local linkage scores for terrestrial wildlife road passage structures for a portion of Massachusetts. The color of the lines is proportional to the change in “connectedness” that would be achieved by the construction of a wildlife passage structure. The darker the color the greater the benefit of using a passage structure.

Based on these restoration scores, road segments can be ranked and prioritized for restoration (**Fig. 7**).

As with dams and road-stream crossings, it is important to be aware of the major sources of uncertainty in the road passage restoration scores:

- As with dams and road-stream crossing, data gaps and errors inherent in the source data are a major concern. Both errors of omission and commission in the roads data are known to exist. Terrestrial barrier scores are intended to reflect the physical and psychological impediments to wildlife movement from roads; the scores are assigned by road class (e.g., motorway, primary road, secondary road, tertiary road, local road, track) based on the average physical characteristics of each road class, but they don't take into account local information (due to the lack of data) about the physical character of the road, nor do they account for other sources of physical barriers to wildlife movement such as Jersey barriers and fencing. Road traffic rates (Gibbs transformed to range 0-1) are intended to reflect the probability of getting killed when trying to cross the road and are based on interpolated traffic rates that are quite noisy; thus, the modeled traffic rate may not accurately reflect the actual traffic rate on a road segment.
- The road passage restoration score represents the potential gain in local connectivity from installing a single wildlife passage structure without considering other potential nearby restoration actions to improve connectivity. Due to the computational challenges we did not consider the benefit of installing multiple road passage structures in nearby locations, but it is quite possible that there would by synergy in installing multiple structures. This remains an important item for future model improvement
- Terrestrial barrier scores for road-stream crossing cells are assigned based either on an algorithm applied to field-based measurement of the crossing or very noisy predictions from a statistical model based on GIS data, and the vast major of crossing scores are based on the statistical model. Thus, the modeled terrestrial barrier score may not accurately reflect the actual terrestrial passability of the road-stream crossing.
- The road passage restoration scores do not take into account the combined benefits of installing a terrestrial wildlife passage structure at a road-stream crossing, and thereby increase both terrestrial connectedness and aquatic connectedness with the same structure. Clearly, all other things being equal, placing a road passage structure at a close-by road-stream crossing makes perfect sense since the potential gains in connectivity are much greater. The current critical linkages analysis does not address this scenario, but it remains an important topic for future model improvements.

5.4 Regional conductance

Regional conductance measures the total amount of ecological flow through a cell from nearby nodes (i.e., core areas) and is a function of the size and proximity of the nodes and the resistance of the focal cell and the intervening landscape between the focal cell and the nearby nodes. Regional conductance differs from local conductance in that it is based on a designated core area network and measures the amount of ecological flow between the designated cores (nodes).

We assessed the regional conductance between each pair of nodes using a new approach, random low-cost paths. It would be straightforward to connect one or more points in each node to one or more points in each neighboring node with a least-cost path; however, there are a number of drawbacks to using least-cost paths. They typically select unrealistically narrow corridors (e.g., one cell wide — something that would be unlikely to be used by most migrating or dispersing animals). As a result, least-cost paths are very sensitive to small GIS errors. They also ignore the number of alternatives, failing to distinguish between situations where there is a single path and situations where there are many alternatives. There are significant limits, therefore, to how usefully one can assess landscape connectivity with least-cost paths.

Our approach is to add some random variation to least-cost paths, making them sub-optimal and variable. We believe this approach, which we call random low-cost paths, more realistically represents the way animals move through the landscape, and more completely and robustly describes the connectivity between two areas. Random low-cost paths have three parameters: one that determines how random they are (ranging from deterministic least-cost paths to random walks), and two momentum parameters that determine the grain of randomness. For this project, we selected parameters that gave "reasonable" paths, as there is no direct biological interpretation of these parameters.

Regional conductance is derived from random low cost paths as follows:

1. for each pair of nodes within a designated threshold distance (e.g., 20 km), select a fixed number of random points (e.g., 1,000) within each node (the "from-node"). These random points are stratified by the representation of each macrogroup of ecological communities within the from-node;
2. construct a *random low-cost path* from each of these points to the first point in the same macrogroup encountered in each neighboring node (the "to-node"). If a macrogroup in the from-node doesn't exist in the to-node, that path is dropped. Ultimately, paths are built in both directions between each pair of nodes. For each focal macrogroup (based on cells in the from-node), random low-cost paths are built on a resistant landscape based on cells in that macrogroup in the to-node. This is done by following a resistant kernel built on a number of points in the to-node "uphill" from the from-node. The result is a set of up to, for example, 2,000 random low-cost paths between each nearby (less than the designated threshold distance between node centroids) pair of nodes in the landscape, stratified by macrogroup. Note, stratification by macrogroup insures that connections are made between similar cells, such that it is likely that an animal moving from one node to another would find habitat at its destination. Paths between each pair of points honor the landscape resistance for the macrogroup in the focal cell—thus, a path from a ridgetop cell will favor dry, steep ridgetops, whereas a path from a wetland will favor wetlands and low, wet areas;
3. measure the functional length of each path(i.e., *path length*) by adding the landscape resistance (based on each starting point in the from-node) along the path's length. This gives path functional distance, which integrates the distance travelled by the path in meters with the resistance of the intervening landscape given each cell's ecological distance from the starting cell to each cell along the path. The minimum resistance value is 1.0, so a 1 km long path through cells in an identical setting as the starting cell would have a functional distance of 1,000;

4. convert path functional distance to *path probability of connectivity* using a Gaussian density function based on a bandwidth (standard deviation) representing dispersal ability. As this is a coarse-filter assessment, we are not focusing on individual species; thus, ideally we would use a series of bandwidths (e.g., 2 km, 5 km, and 10 km, with a maximum spread of 2 times the bandwidth) to represent a range of dispersal abilities. However, to minimize the complexity of the results we report only the results of the 10 km bandwidth. Note, the Gaussian function represents a non-linear decay with distance, such that the probability of connectivity declines slowly at first with increasing functional distance and then declines rapidly as the functional distance increases further, and eventually declines to zero. Any path with a functional distance greater than 2 times the bandwidth is dropped; and
5. multiply path probability of connectivity by the mean value of the two nodes, where the value of each node is computed as the sum of the core area selection index (as described in the landscape conservation design document), assign this value to each cell in the path, sum across all paths in the landscape, and let this be the regional conductance index. Note, the sum of the core area selection index is simply a more meaningful indicator of node size that takes into account not only the size of the node but also its quality as represented by the selection index.

As defined above, the regional conductance index is influenced by three major factors. First, the resistance of the focal cell itself, which is a function of its ecological similarity to the cells in the nearby nodes, and the resistance of the intervening landscape between the nearby nodes affects the magnitude of conductance; the greater the resistance of the focal cell and intervening landscape between the nodes, the lower the probability of connectivity of the paths through the focal cell, and thus the lower the regional conductance. Second, the proximity of the nearby nodes affects conductance, since the probability of connectivity decreases according to a Gaussian function of the functional distance between nodes, and nodes beyond a functional distance of 2 times the bandwidth are considered functionally disconnected. Third, the size and quality of the nearby nodes affects conductance, since the path probability of connectivity is weighted by the size and quality of the two nodes connected by the path. Thus, cells with higher values are functionally closer to larger nodes and indicate a greater probability that animals will pass through these cells.

The regional conductance metric is a cell-based measure of connectivity between designated core areas (**Fig.8**). The index is computed for every cell, whether it is between nodes or within a node, but the index is most useful for assessing the conductance between nodes. Cells within nodes can get a conductance value because the random low-cost paths can pass through these cells between the originating cell in the from-node and the terminating cell in the to-node; however, there is a strong bias towards cells near the periphery of the nodes since the paths terminate at the first cell of the corresponding macrogroup encountered in the to-node. In addition, some paths flow completely through a node between two other nearby nodes. Thus, some of the conductance attributed to cells within nodes is attributed to their role in facilitating flows between other nodes. For these, interpreting the conductance values for cells within the nodes is problematic and thus should be avoided. Importantly, this metric is contingent upon the a priori designation of core areas (nodes) and thus is primarily useful in the context of landscape conservation

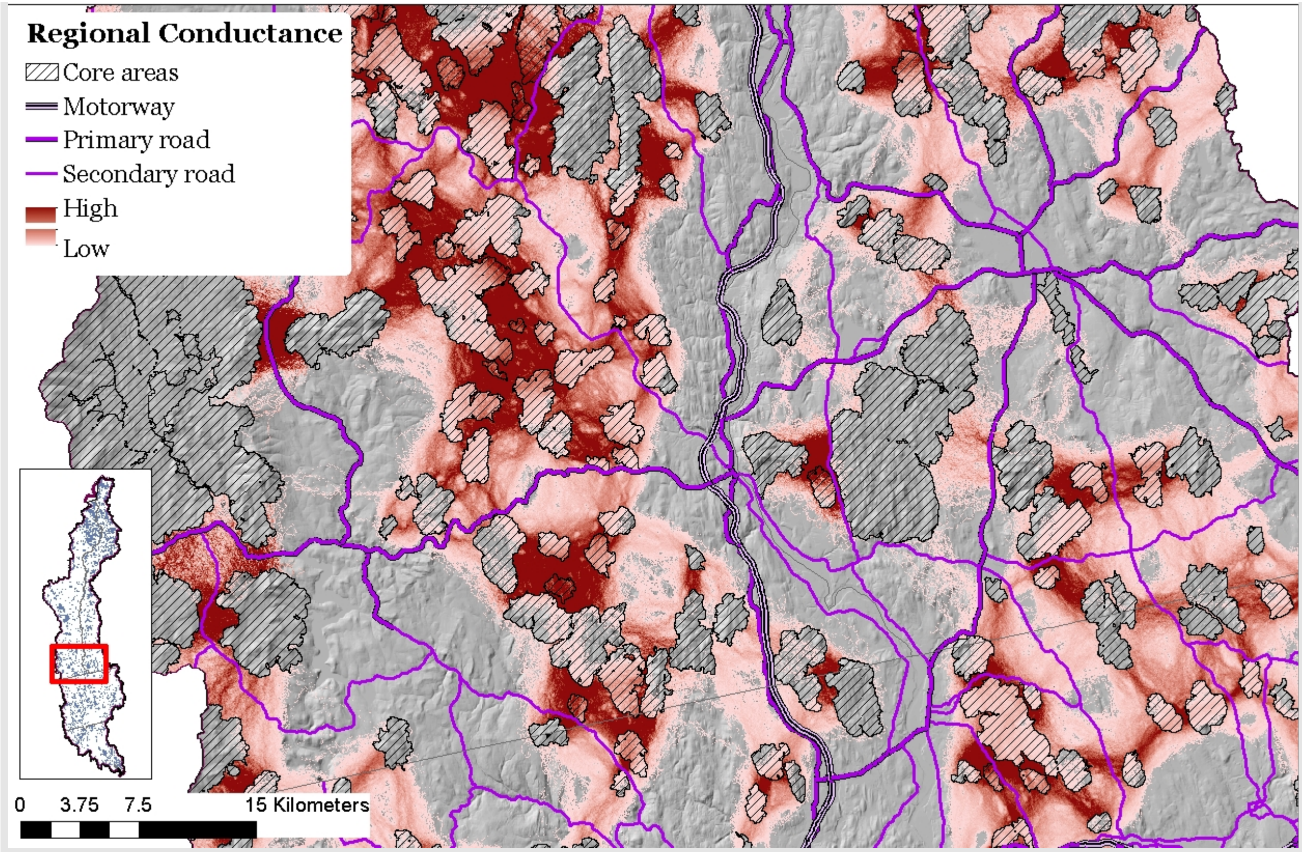

Figure 8. Illustration of the regional conductance metric, shown here for a designated core area network and a small portion of the Connecticut River watershed. Conductance is given by the intensity of red and depicts areas of relatively high predicted ecological flows between designated core areas; major roads are depicted by class.

design. This index is perhaps best used in combination with local conductance (as described earlier) in the context of landscape conservation design in order to provide a single spatially comprehensive assessment of conductance that can be used to identify priority areas for conservation action.

5.5 Regional irreplaceability

Regional irreplaceability measures the concentration of ecological flow between nearby nodes going through a cell. Irreplaceability does not indicate whether a cell is irreplaceable or not in an absolute sense, since there are almost always alternative pathways between nodes. Rather, it is a function of the proportion of the random low-cost paths between two nodes that go through each cell independent of the size and proximity (up to a limit) of the nodes; a cell that accounts for a large proportion of the paths is relatively irreplaceable. Whereas regional conductance reflects how much flow is likely to occur through a cell (i.e., its ecological importance in promoting connectivity), which is strongly influenced by the size and proximity of nearby nodes as well as the resistance of the intervening landscape, regional irreplaceability measures the proportion of the flow paths between nodes that go through a cell regardless of the size and proximity (up to a limit) of nearby nodes. Thus, regional irreplaceability reflects the relative importance of a cell to flow if it were to occur, but does not reflect how much flow is likely to occur or be lost if that cell were developed. Cells within a relatively wide "corridor" between two nodes will have low irreplaceability because there are a lot of alternative paths between the nodes. Conversely, a cell that is a "pinchpoint" of low resistance between two nodes will have high irreplaceability because most of the paths are likely to go through that cell.

Regional irreplaceability is computed as the proportion of the maximum number of random low cost paths between two nodes that traverse a focal cell, as follows:

1. for each pair of nodes within a designated threshold distance (e.g., 10 km), build a user-specified number (e.g., 1,000) of random low-cost paths (see above for details) in each direction (i.e., from node A to B and from node B to A);
2. for each cell tally the number of random low-cost paths that traverse the cell; and
3. divide the observed tally by the maximum possible tally (e.g., 2000). Note, if a cell is traversed by random low-cost paths from more than one pair of nodes, then take the maximum observed proportion between any pair of nodes and let this be the regional irreplaceability index.

As defined above, the regional irreplaceability index is influenced primarily by the resistance of the focal cell relative to the resistance of the intervening landscape between the nodes and its geographic position between nodes. A cell positioned along a narrow "corridor" of low resistance between nodes will have a high degree of irreplaceability because most of the random low-cost paths will flow through that location. Conversely, a cell positioned in a broad "corridor" of low resistance or well away from the direct path between nodes is likely to have lower irreplaceability. Importantly, irreplaceability is affected only indirectly by the size and proximity of nearby nodes; all other things being equal, a cell positioned directly between two small and proximate nodes is more likely to be traversed by paths than a cell positioned directly between two large and distant nodes, because in the latter case the paths are more likely to start from more widely spaced cells and have more opportunity to randomly walk between the nodes without traversing the focal cell.

The regional irreplaceabilty metric is a cell-based measure of connectivity between designated core areas (**Fig.9**). The index is computed for every cell, whether it is between nodes or within a node, but the index is most useful for assessing the irreplaceability of cells between nodes. Like regional conductance, cells within nodes can get an irreplaceability value, but interpreting these values should be avoided for the same reasons as discussed above. Importantly, like regional conductance, this metric is contingent upon the a priori designation of core areas (nodes) and thus is perhaps best used in combination with regional conductance in the context of landscape conservation design in order to provide a single spatially comprehensive assessment of regional connectivity that can be used to identify priority areas for conservation action.

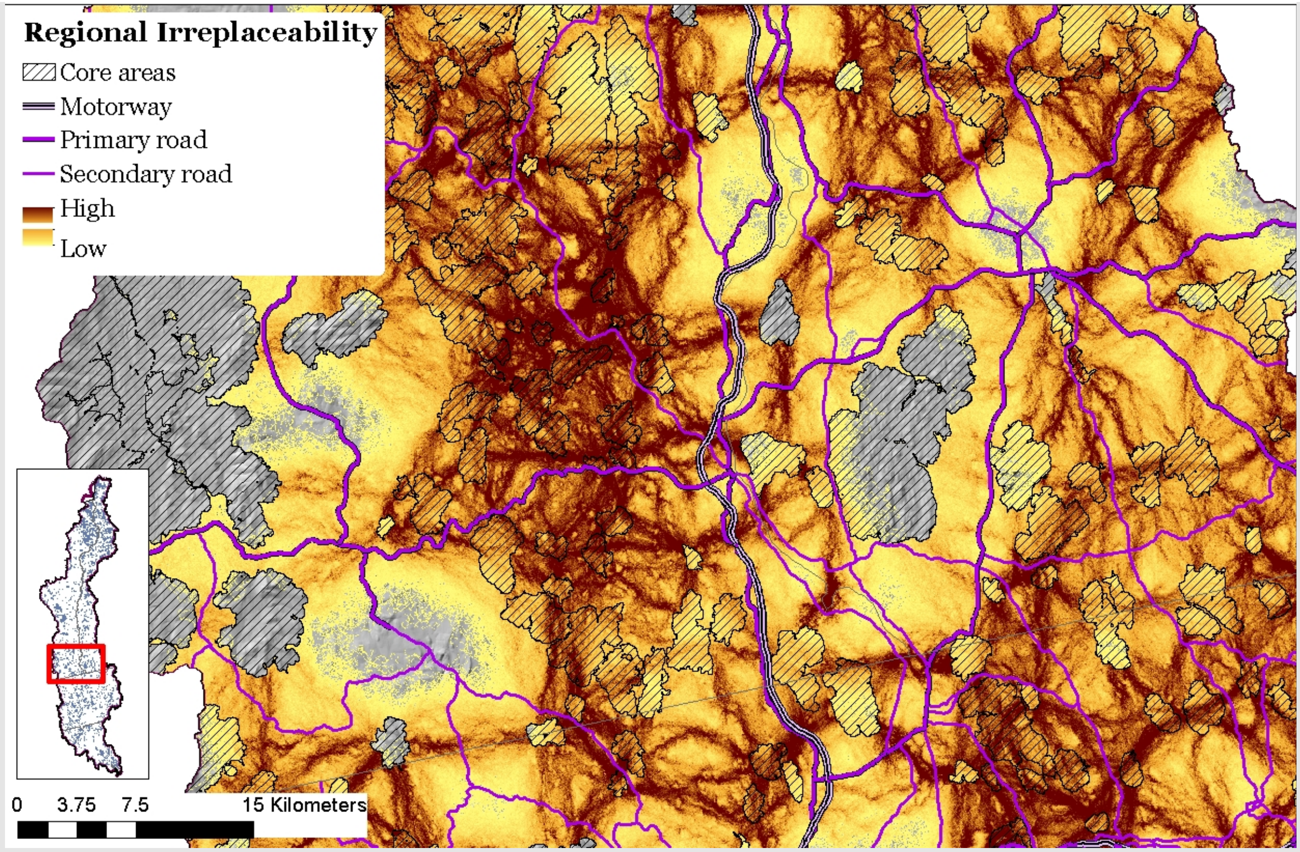

Figure 9. Illustration of the regional irreplaceability metric, shown here for a designated core area network and a small portion of the Connecticut River watershed. Irreplaceability is given by the intensity of brown and depicts the proportion of random low-cost paths between designated core areas that traverse each cell; major roads are depicted by class.

5.6 Regional vulnerability

Regional vulnerability measures the vulnerability of an irreplaceable cell with high regional conductance to the loss of its connectivity value caused by future development, and is a function of regional conductance, regional irreplaceability and the integrated future probability of development. Cells with relatively low regional conductance and/or irreplaceability have low vulnerability regardless of their risk of development, since regional connectivity will not be degraded too much if they get developed. On the other hand, cells with relatively high regional conductance that are irreplaceable will have high vulnerability if they suffer high risk of development, since regional connectivity will be seriously degraded if they get developed.

Regional vulnerability is computed as the product of regional conductance, regional irreplaceability and the integrated probability of development (as described previously). Thus, as any one of the components goes to zero, then the product goes to zero, and the product is only large when all three components are large. Consequently, regional vulnerability is greatest where there is high regional conductance and irreplaceability; i.e.,

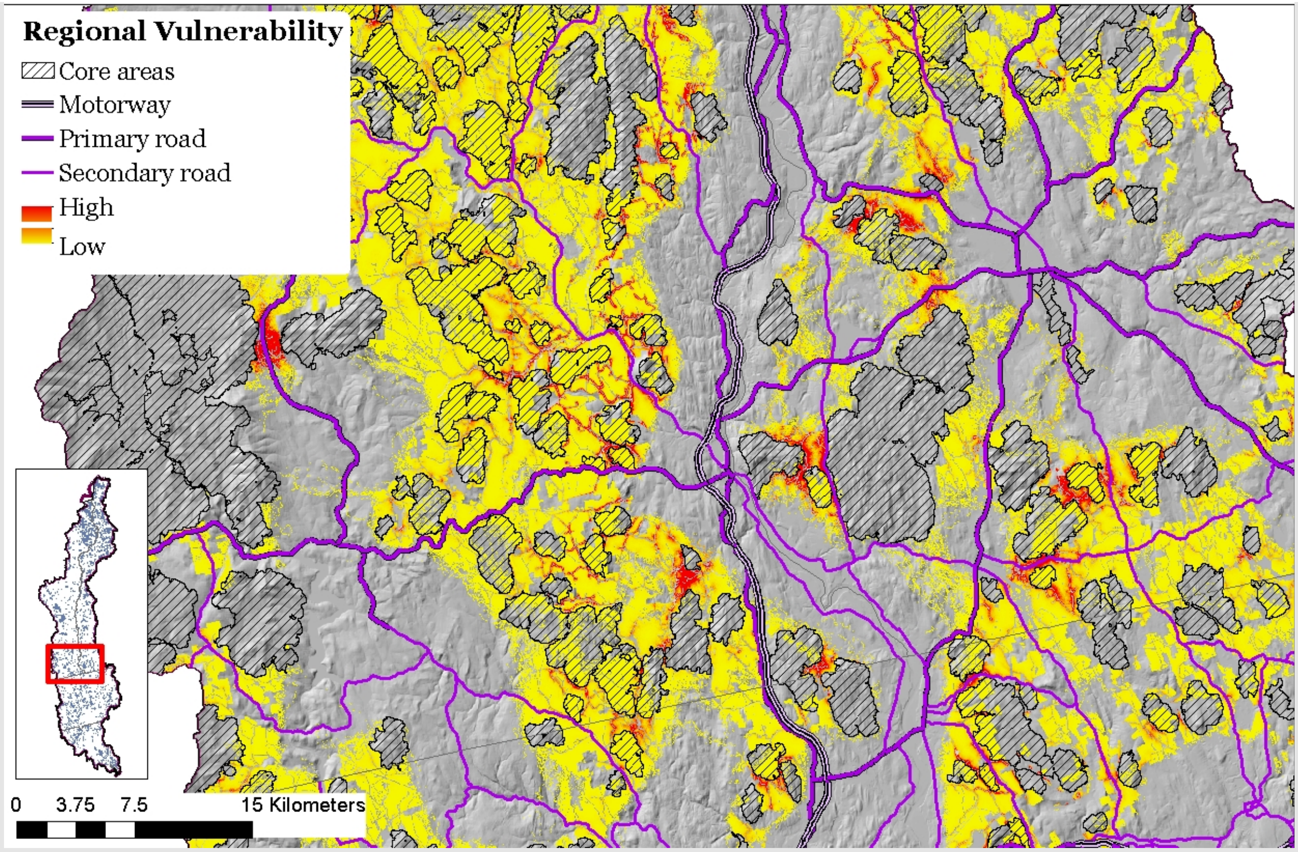

Figure 10. Illustration of the regional vulnerability metric, shown here for a designated core area network and a small portion of the Connecticut River watershed. Vulnerability is shown here as a gradient from low (yellow) to red (high) and represents the relative probability of cells with high regional conductance that are irreplaceable being developed in the future; major roads are depicted by class.

in narrow "corridors" of ecologically similar areas with minimal current development between large nearby nodes (core areas), and where there is also relatively high probability of development in the future.

The regional vulnerability metric is a cell-based measure of connectivity between designated core areas (**Fig.10**). The index is computed for every cell, whether it is between nodes or within a node, but the index is most useful for assessing the vulnerability of cells between nodes. Like regional conductance and irreplaceability, cells within nodes can get a vulnerability value, but interpreting these values should be avoided for the same reasons as discussed above. Importantly, like regional conductance and irreplaceability, this metric is contingent upon the a priori designation of core areas (nodes) and thus is perhaps best used in combination with local vulnerability in the context of landscape conservation design in order to provide a single spatially comprehensive assessment of regional connectivity that can be used to identify priority areas for conservation action.

5.7 Critical nodes/links

As noted above, the regional connectivity analysis depends on the designation of a core area network in which the network consists of a set of nodes (core areas) connected via abstract linkages (i.e. areas of high regional conductance). Our critical node/linkage analysis measures the relative contribution of each node and link to regional connectivity; specifically, the change in the connectivity of the entire network if the node or link were removed. Critical nodes and links are disproportionately important to the connectivity of the entire network, either due to their size (nodes), amount of ecological flow (links), or their geographic location in the network.

To compute node/link importance scores, the landscape is first translated into a "graph", based on a graph-theoretic framework (Urban and Keitt, 2001), in which nodes are connected by links (note, in the graph theory literature, links are called “edges,” but we consider this term too confusing, and use “links” instead). The designated core areas are used as the nodes, with a value based on the sum of the core area selection index (which serves as an index of node size and quality). The links between nodes are defined as the mean path probability of connectivity (see previous description). Specifically, we multiply path probability of connectivity by the mean value of the two nodes, where the value of each node is computed as the sum of the core area selection index, and compute the average across paths. Note, link probabilities between pairs of nodes is asymmetrical, since the link probability need not be the same in both directions of movement.

Given the graph theoretic representation above, node/link importance is determined as follows:

1. for the constructed graph, compute the network *Probability of Connectivity* index (*PC*, Saura and Pascual-Hortal, 2007) to assess connectivity of the overall network as follows:

   $$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^*}{A_L^2}$$

   where n is the number of nodes, a_i and a_j are values of nodes i and j (i.e,. sum of the core area selection index), p_{ij} are link probabilities between nodes i and j, A_L is the value of the full landscape (i.e., sum of the core area selection index across all nodes), and p^*_{ij} is the maximum joint probability of all possible paths between nodes i and j.

2. remove each node and link in turn and calculate the difference in *PC* (ΔPC) to assess the importance of each node and each link to overall network connectivity.

PC is based on the value (i.e., size and quality) of nodes and the probability of links between them in a graph framework. *PC* is defined as the probability that an animal in a random node would be able to traverse the network to any other given node in the landscape. Distant nodes are connected via stepping stones, and the probability of these connections is the maximum joint probability of links connecting the two nodes. *PC* gives a robust and meaningful measure of the connectivity of a landscape (as represented by a network). It ranges from 1.0 for a landscape that occurs entirely within a single node, to near 0 for highly disconnected landscapes. ΔPC can be used to represent the difference between two actual landscapes, between a landscape at a current and future time, or between a landscape and a modification of the same landscape. Here, we use ΔPC to assess node and link importance by virtually modifying the same landscape via the removal of each node/link.

We compute and report the following metrics for each node (core area):

- **import10k** = ΔPC based on a 10 km threshold distance for regional conductance (as described previously). Note, node import10k reflects the influence of both node value (i.e., sum of the core area selection index) and node position in the network; nodes with greater value (as represented by the sum of the core area selection index) and those strategically positioned in the network have greater values of this metric.
- **importRank** = rank of import10k (1 = largest ΔPC) based on standard competition ranking.
- **relImport** = ΔPC computed without considering node value (i.e., sum of the core area selection index) in the calculation of PC; this involves setting all a_i and a_j in the calculation of PC to 1. Since ΔPC is heavily influenced by node value, relImport gives more influence to node position in the network.
- **relImpRank** = rank of relImport (1 = largest relImport) based on standard competition ranking.

We compute and report the following metrics for each link:

- **import10k** = ΔPC based on a 10 km threshold distance for regional conductance (as described previously). Note, link import10k reflects the influence of both the functional length of the link (as represented by the link probability of connectivity) and the value (i.e., sum of the core area selection index) of the nodes being connected; links with shorter functional distance (i.e., greater link probability) and connecting nodes with greater value (as represented by the sum of the core area selection index) have greater values of this metric.
- **importRank** = rank of import10k (1 = largest ΔPC) based on standard competition ranking.

The results of this analysis are presented in schematic "ball-and-stick" diagrams (**Fig. 11**). They identify nodes and links that are important for landscape connectivity because they both contribute to overall connectivity and are non-redundant, such that their loss would greatly reduce overall landscape connectivity. Node and link importance scores can be used in the context of landscape conservation design to identify priorities for conservation action.

6 Alternatives Considered and Rejected

We did not seriously consider any alternatives to the overall regional connectivity modeling approach described here. However, we did evaluate many alternatives for parameterizing the random low-cost path algorithm, including varying the three parameters that control the randomness and momentum of the paths, and the bandwidth of the Gaussian

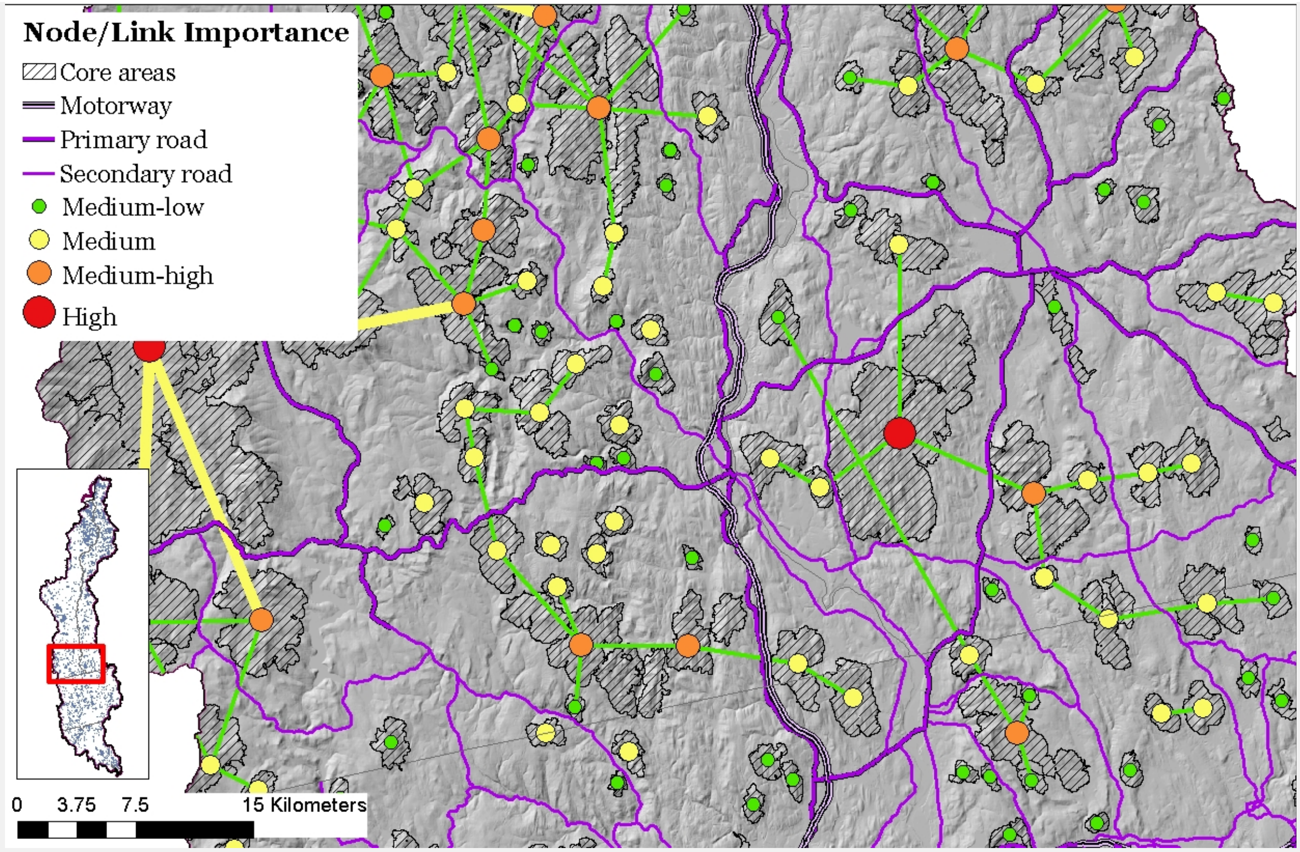

Figure 11. Illustration of the critical node/link analysis, shown here for a designated core area network and a small portion of the Connecticut River watershed. Core importance is depicted by the size and color of the points centered on each node (core area); link importance is similarly depicted by the size and color of the lines connecting the nodes; only nodes and links of medium-low to high importance are shown. Both core and link importance reflect the change in regional connectivity resulting from removal of that core or link. Major roads are depicted by class.

transformation of path functional distance to path probability of connectivity, and settled on parameters that provided reasonable random walk behavior and at an intermediate scale (i.e. 10 km bandwidth). Smaller and larger bandwidths do provide insights into connectivity at different scales, and perhaps better reflect the multi-scale nature of connectivity, but incorporating multiple scales of connectivity into the assessment created too many practical challenges to the display and interpretation of results, so we settled on an intermediate scale that is perhaps relevant to a majority of species for which connectivity is an issue. In addition, we explored the differences between equal versus proportional representation of macrogroups in building random low-cost paths, and settled on the latter as more meaningfully representing conductance (and its derivatives) for the ecosystem as a whole.

We recognize that our local and regional connectivity assessment reflects an ecosystem-based perspective, as resistance is defined based on ecological similarities between locations, and may not adequately represent functional connectivity for any particular species. While a species-specific approach is feasible with our current modeling approach (i.e., resistance can be defined separately for each species), we did not have the resources available to implement a multi-species connectivity assessment for this phase of the project. However, this remains an important issue to be considered in future phases of this project.

7 Major Implementation Constraints

The major implementation constraint is time and computational resources. These connectivity models are computationally intensive, requiring several hours of computing on our computer cluster to complete a single regionally connectivity assessment for the Connecticut River watershed. Similar assessments for the entire Northeast extent have not been attempted yet, but surely will require considerable computing resources. Thus, it is not practical to run multiple scenarios in order to evaluate multiple alternative core area network designs.

8 Major Risks and Dependencies

The major risk with our local and regional connectivity assessment is that the ecosystem-based approach we utilize (at least currently) may not represent connectivity meaningfully for any single focal species, since it has not been optimized for that species. Thus, the linkages between conservation nodes that we identify may not actually function as the linkages for a particular species and thus our conservation attention may not be directed to the place where it will be most effective. On the other hand, given the practical impossibility of modeling every species separately due to limitations in data, knowledge and computing power, it seems reasonable to assume that the ecosystem-based approach applied here is the most likely to address connectivity for the most species.

It is important to recognize that our regional connectivity assessment is based on a designated core area network. Thus, the connectivity results are ultimately only as good as the core are network that they apply to. Given the myriad possibilities for creating core areas, this means that there are myriad variations in the regional connectivity results.

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